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Mental extrapolation of target position is strongest with weak motion signals and motor responses

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Abstract

Some accounts hold that the position of moving objects is extrapolated either in visual perception or visual short-term memory ("representational momentum"). However, some studies did not find forward displacement of the final position when smooth motion was used, whereas reliable displacement was observed with implied motion. To resolve this conflict, the frequency of position changes was varied to sample motion types between the extreme cases of implied and smooth motion. A continuous function relating frequency of target change and displacement was found: Displacement increased when the frequency of position changes was reduced. Further, the response mode was varied. Probe judgments produced less forward displacement than motor judgments such as mouse or natural pointing movements. Also, localization judgments were susceptible to motion context, but not to variations of probe shape or expectancy about trajectory length. It is suggested that forward displacement results from the extrapolation of the next step in the observed motion sequence.

Keywords: Representational momentum; Position judgments; Motion; Extrapolation; Memory; Flash lag; Pointing

1. Introduction

At least two different lines of research have suggested that the visual system extrapolates the position of moving objects. First, it was suggested that the visual system extrapolates the position of moving objects in order to compensate for neural transmission delays (Nijhawan, 1994, 2002). Consistent with *perceptual extrapolation*, the position of a briefly-flashed stationary object was seen to lag the position of a physically aligned moving object. However, a number of studies on the flash-lag effect were at odds with perceptual extrapolation (overview in Krekelberg & Lappe, 2001). Among other things, it was found that a flash appeared aligned with the final position of a smoothly moving, sharp-edged target (Baldo, Kihara, Namba, & Klein, 2002; Eagleman & Sejnowski, 2000; Kerzel, 2000; Whitney, Murakami, & Cavanagh, 2000). Perceptual extrapolation would predict that the perceived final position was beyond the true final position.

Second, it was suggested that the position of moving objects is extrapolated in visual short-term memory (overview in Hubbard, 1995b). After offset of a moving target, extrapolation displaces the remembered final target position in the direction of motion. A cognitive approach holds that forward displacement (FD) of the final position of a moving target results from the inability to stop extrapolation instantaneously ("representational momentum"). Because reference is made to rather high-level cognitive processes, the term *mental extrapolation* is used to refer to extrapolation in visual short-term memory. The current paper explores effects of motion type, motion adaptation, and perceptual set on mental extrapolation. Whereas strong effects of motion type and response mode were observed, effects of perceptual set were inconsistent, and effects of motion adaptation were absent.

1.1. Effects of motion type

To investigate FD of the final target position, some authors used linear, smooth target motion that resembled real natural motion (see Fig. 1D, e.g., Hubbard & Bharucha, 1988). Smooth motion on a monitor is

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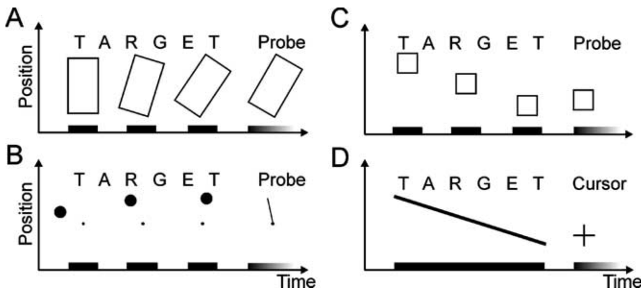

Fig. 1. Overview of the different methods used to study representational momentum. The methods are characterized in space–time coordinates. Black boxes on the time-axis indicate that the target or probe was shown. *Panel A*: A target rectangle was presented three times at the same position on the screen. Between successive presentations, the target was blanked and rotated by 17°. After the final target view, a probe rectangle was shown and observers were asked to indicate whether the probe was at the same orientation as the final target rectangle. The probe remained visible until a judgment was made. This paradigm was mostly used by Freyd and colleagues (e.g., Freyd & Finke, 1984). *Panel B:* A variant of the method shown in panel A. A single disk rotates around the fixation point. A line is used as a probe stimulus. Observers are asked to indicate whether the probe is displaced in or opposite to motion. This paradigm was used in Experiment 1. *Panel C:* The method is as in panel A, but the target translates. Observers are asked to judge whether the probe is at the same position as the target. Various authors used these methods (e.g., Halpern & Kelly, 1993; Nagai & Yagi, 2001; Reed & Vinson, 1996). *Panel C:* The target changes its position continuously without noticeable jumps. As it is continuously visible (within the limits imposed by the refresh rate of the monitor), the impression of smooth motion is conveyed. After target offset, observers are asked to indicate the final position by moving a cross-hair mouse cursor to the final target position. This method was used mainly by Hubbard and colleagues (e.g., Hubbard & Bharucha, 1988). With smooth pursuit of the target, the judged final target position and the eyes are displaced in the direction of target motion relative to the true final target position. In contrast to the paradigms presented in panels A–C, displacement of the final target position only occurs if observers pursue the target with their eyes.

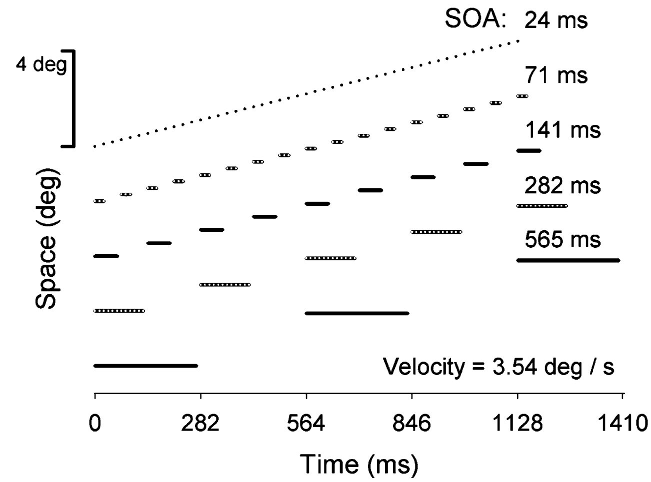

Fig. 2. Different motion types are shown in a space–time plot. The solid lines indicate target presentation times. When the stimulus onset asynchrony (SOA) between successive target positions was large, implied or apparent motion resulted. The smaller the SOA, the smoother the stimulus motion appeared. In Experiments 1d, 2, and 3, the five different SOAs were presented. If the trajectory length and velocity is fixed, the total time necessary to pass through a certain distance will vary as a function of SOA, because the target presentation time increases with SOA (it is always about half the SOA). However, a control experiment (not reported) showed that the results were not affected by target presentation time.

created by shifting the target from one position to the next at a very high frequency (see Fig. 2) such that the stimulus onset asynchrony (SOA) between successive target presentations is small. With linear smooth target motion pursuit eye movements are very likely (Yasui & Young, 1975). After smooth pursuit of a moving target that suddenly disappears, the eyes overshoot the final target position such that the fovea is displaced in the direction of motion relative to the final target position. It was argued that a tendency to localize objects toward the fovea and visible target persistence contribute to FD after pursuit of a smoothly moving target, mainly because FD was absent when observers did not follow the moving target with their eyes, but maintained fixation on a stationary object (Kerzel, 2000; Kerzel, Jordan, & Müsseler, 2001). Alternatively, it may be that observers fail to use the extra-retinal signal such that the oculomotor overshoot goes unnoticed (cf. Brenner, Smeets, & van den Berg, 2001).

In contrast, other authors used implied rotational or linear motion and reported reliable FD (see Fig. 1A–C, e.g., Freyd & Finke, 1984; Reed & Vinson, 1996). To create implied motion, the target position is changed infrequently, and blank intervals are inserted between successive target presentations. In a large number of studies on "representational momentum", the target was shown in one position for 250 ms and after a 250 blank interval, it was shown in the next position. Thus, the SOA between successive target positions was 500 ms which gives the impression of a target appearing at different locations. With implied motion, pursuit eye movements and subsequent oculomotor overshoot are highly unlikely (Churchland & Lisberger, 2000), and a recent study reported no systematic dependency of FD on eye movements: When eye movements were measured during a sequence of implied motion, no systematic relation between shifts of fixation and FD was revealed (Kerzel, 2003a).

Thus, there is an unresolved conflict between studies using smooth target motion and studies using implied motion. Across studies, the results are consistent with the hypothesis that smooth motion does not produce FD of the final target position in the absence of eye movements, whereas implied motion does. However, a direct comparison of the two motion types in a single study is missing. Also, there is no study that evaluated displacement with motion types between the two extreme cases of implied and smooth motion. It has long been known that the impression of motion varies with the temporal interval between target presentations. For example, Graham (1965) found that two flashes separated by a temporal interval smaller than 30 ms were perceived as simultaneous. Partial movement was seen with intervals between 30 and 60 ms. Apparent motion resulted when the interval was between 60 and 200 ms, and mere succession was perceived with longer intervals than 200 ms (see also Steinman, Pizlo, & Pizlo, 2000; Wertheimer, 1912). Thus, it remains to be investigated whether FD occurs with partial and apparent motion.

1.2. Effects of response mode

Another discrepancy between studies on FD that used smooth and implied motion is the response mode. Whereas probe judgments were used in Freyd's original work (e.g., Freyd & Finke, 1984, 1985; Freyd & Johnson, 1987), later investigator also used (mouse) pointing responses (e.g., Hubbard, 1995a; Hubbard & Bharucha, 1988; Hubbard & Motes, 2002). There is evidence that the type of response influences localization judgments: Objects that are presented briefly before saccade onset are localized toward the saccade goal with probe judgments (Ross, Morrone, & Burr, 1997), but not with pointing movements (Burr, Morrone, & Ross, 2001). In the absence of eye movements, the onset position of a moving target is localized in the direction of motion with probe judgments, but opposite to motion with mouse pointing (Kerzel, 2002a). Thus, it may be that localization of the offset position is also influenced by the response mode. There are some hints that this may be the case: There was not even the slightest evidence for FD when the eyes were motionless and the offset position of a smoothly moving target had to be compared to a probe stimulus (Baldo et al., 2002; Eagleman & Sejnowski, 2000; Kerzel, 2000; Whitney & Cavanagh, 2002; Whitney et al., 2000). Rather, there was a tendency for backward displacement in some studies (Baldo et al., 2002; Kerzel, 2000). However, when observers had to (mouse-) point (Kerzel et al., 2001) or look (Kerzel, 2003b) at the final position of a smoothly moving target, there was small, (marginally) significant FD. Thus, there is reason to believe that the response mode may influence judgments of the final target position.

1.3. Motion adaptation

Further, the study looked at a problem associated with probe judgments and implied motion (for in-depth discussion, see Bertamini, 2002). It is known that exposure to apparent or implied motion in a particular direction increases the threshold for the detection of motion in the same direction (e.g., Pantle, Gallogly, & Piehler, 2000). Thus, the detection of implied motion between the final target and the probe position would be harder in the same direction as previous motion than in the opposite direction. If observers partially based their judgments on the perceived motion between the final target and the probe position, more "same" judgments would be given to probes displaced in the direction of motion because thresholds are higher in this direction. One prediction of this idea is that probes that minimize (residual) motion signals between the final target presentation and probe presentation should decrease FD. Also, motor judgments that do not use a reference stimulus should decrease or eliminate FD.

1.4. Perceptual set

In most studies that have looked at FD with implied motion, the length of the trajectory was fixed, and observers knew where the target would appear and vanish before a trial started (e.g., Freyd & Finke, 1985; Freyd & Johnson, 1987; Freyd & Jones, 1994). In a recent study, expectations about what an observer would see on a given trial were manipulated by using different designs (Kerzel, 2002b). Both the direction of motion and the target's starting position were treated either as fixed or random variables. It turned out that FD was eliminated when both the target's starting position and the direction of motion were unpredictable. Thus, it may be that expectations about the target's motion that developed across trials (i.e., perceptual set) contribute to FD. However, this conclusion may be limited to the stimulus type investigated: In Kerzel (2002b), the rotation of a rectangle formed by 8 dots was shown. It is unclear whether these results generalize to a simpler stimulus, such as a single disk. Nonetheless, it is unclear whether FD with implied motion may obtain with (a) random trajectory length and (b) unpredictable direction of motion and starting position.

1.5. Overview of study

The goal of the present investigation was to further investigate effects of motion type, response mode, motion adaptation, and perceptual set. The major manipulations and results are summarized in Table 1. In Experiments 1–3, different types of rotational motion were presented. The SOA between successive target positions was systematically varied. In Experiment 1, probe judgments and an adaptive method were used to estimate the final position. Different probe stimuli were presented that maximized or minimized implied motion between the final target and the probe stimulus. In Experiments 2 and 3, motor responses (mouse and real pointing) were employed. In Experiments 1 and 2, the trajectory length was either fixed or random and the different motion types were either shown randomly interleaved, or in separate blocks of trials.

Table 1
Overview of experimental manipulations and results

Manipulation	Experiment 1a–d	Experiment 2a and b	Experiment 3
Perceptual Set			
Trajectory length	No (1a, 1d)	–	–
Motion type	Yes (1a/b vs. 1d)	Yes (2a vs. 2b)	–
Motion adaptation	No (1a, 1d)	No (1 vs. 2)	–
Motion type	Yes (1a, 1b, 1d)	Yes (2a, 2b)	Yes
Response mode	–	Yes (1 vs. 2)	Yes (1 vs. 2, 2 vs. 3)
Retention interval	No (1c)		

Perceptual set was manipulated by fixing a variable at a constant value within a block, or by randomly changing it from trial to trial. This was done for trajectory length and motion type. Effects of motion adaptation were investigated by comparing different probe stimuli. Motion type was manipulated by varying the SOA between successive target presentations. Response mode varied between probe (Experiment 1) and motor judgments (Experiments 2–3).
"Yes" indicates that the experimental manipulation had an effect. "No" indicates that it did not. The numbers indicate in which experiment the manipulation was run, and whether the comparison was done within or between experiments (marked by vs.).

2. Experiment 1a–d: Probe judgments

In Experiment 1, observers were asked to memorize the final position of a disk moving on a circular trajectory (see Fig. 1B). An adaptive method was used to adjust the position of a probe stimulus to the remembered final position. [1] The following manipulations were carried out: (1) To examine effects of motion type on offset localization, the SOA between successive target presentations was varied. In Experiment 1a–c, the SOAs were 565, 24, and 565 ms, respectively. In Experiment 1d, a range of SOAs between 24 and 565 ms was presented randomly interleaved. (2) To examine effects of motion adaptation, one of two probe stimuli was used. A line that extended from the center of rotation to the orbit of the circular trajectory minimized implied motion between target and probe (see Fig. 1B). In contrast, a disk similar to the target that appeared on the circular orbit maximized implied motion between target and probe. (3) To examine effects of predictability, the length of the trajectory was either fixed or varied randomly. (4) Further, the retention interval between target offset and probe onset was manipulated in Experiment 1c to see whether there is a time course of FD. Freyd and Johnson (1987) found that FD increases up to 250 ms and decreases beyond 250 ms. Other researchers failed to find this pattern (Finke & Freyd, 1985; Halpern & Kelly, 1993; Kerzel, 2002b) and reported constant FD across retention intervals. The largest range of intervals measured so far was 250–2000 ms in Finke and Freyd (1985).

2.1. General methods

2.1.1. Participants

Students at the Ludwig-Maximilians University of Munich were paid for their participation. Participants reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment.

2.1.2. Apparatus

The stimuli were presented on a 21″ (diagonal) display with resolution of 1280(H)×1024(V) pixels and a refresh rate of 85 Hz. One pixel measured 1.8 min of arc (arcmin). The horizontal position of the left eye was monitored with a head-mounted, infrared, light-reflecting eye tracker (Skalar Medical B. V., IRIS Model 6500). The analog signal was digitized at a rate of 250 Hz by a DataTranslation A/D-D/A converter (DT 2821). Observers' head position was stabilized with a chin and cheek rest. The apparatus was calibrated before each experimental block started.

2.1.3. Stimuli

A black disk with a diameter of 30 arcmin was used as target. The target moved on a circular orbit with a radius of 3° at a velocity of 3.5°/s. The SOA between successive stimulus presentations was set to 24, 71, 141, 282, or 565 ms such that the target position was changed at a frequency of 42.55, 14.16, 7.08, 3.54, or 1.77 Hz (see Fig. 2). Two probe stimuli were used: A line that extended from the fixation point to the imaginary circle traced by the target (see Fig. 1B) or a red disk with a diameter of 30 arcmin that appeared on the imaginary circle.

2.1.4. Design, procedure and results

A PEST procedure (Lieberman & Pentland, 1982) adjusted the orientation of the probe so it appeared at the remembered final position of the target (i.e., the point of subjective equality, PSE). Four estimates of the PSE based on 18 trials were collected for each motion condition. Half of the PEST staircases approached the PSE from positions lying in the direction of motion, and the other half from positions opposite to motion. The deviation of the probe from the true final position was measured in degrees of rotation and 10 degrees of ro-

[1] Similar results were obtained with linear motion and the method of constant stimuli. For brevity, these experiments were not included in the present report.

tation corresponded to about 0.5° of visual angle. The direction of motion and starting position of the target were randomized. Observers were asked to judge whether the probe was displaced in or opposite the direction of motion relative to the final target position. Positive and negative displacement values indicate that the judged final position deviated in and opposite the direction of motion from the true final position, respectively. Mean displacement for Experiments 1–3 is shown in Table 2 and Fig. 3. *T*-tests comparing the means to zero are shown in Table 2.

2.2. Experiment 1a: Implied motion, perceptual set, motion adaptation

Only a single motion type was presented. Successive target positions were separated by an SOA of 564 ms. Observers worked through two blocks of 72 trials each which yielded eight estimates of the PSE based on 18 trials. The probe stimulus (line vs. disk) was changed between blocks and the order of blocks was counterbalanced across subjects. For twelve observers, the trajectory length was fixed at 4° and for another twelve students it varied randomly between 2°, 4°, and 6°.

A mixed-factors ANOVA (variability of trajectory length × probe stimulus) showed that there was no effect of probe stimulus (line vs. disk) and variability of trajectory length (fixed vs. random). Forward displacement ($M = 5.57$ degrees of rotation) was significantly different from zero.

2.3. Experiment 1b: Smooth motion

The same methods as in Experiment 1a were used, but a different motion type was shown. Successive target positions were separated by an SOA of 24 ms. The resulting motion looked smooth and continuous. The trajectory length was fixed at 4°. Twelve students participated.

A *t*-test revealed that the two probe stimuli (line vs. disk) did not differ. Forward displacement was not significantly different from zero ($M = -0.54$ degrees of rotation). In a mixed-factors ANOVA (experiment × probe stimulus), mean forward displacement in Experiment 1b (SOA = 24 ms) was significantly different from mean forward displacement in Experiment 1a (SOA = 564 ms), $F(1,22) = 7.41$, $MSE = 521.02$, $p < 0.05$.

2.4. Experiment 1c: Implied motion, retention interval

Target position changed with an SOA of 564 ms. The retention interval (i.e., the time between target offset and probe onset) varied between 282 and 564 ms. Four estimates of the PSE based on 18 trials were collected for each retention interval and observer. Data were collected in a single block of 144 trials. Only the line probe was used. Twelve students participated.

There was no significant difference between the two retention intervals, $t(11) = -1.68$, $p = 0.12$. Forward displacement was not significantly larger with the long compared to the short SOA ($M = 3.90$ vs. 2.39 degrees of rotation). Overall, forward displacement was significantly different from zero ($M = 3.14$ degrees of rotation).

2.5. Experiment 1d: Motion type, perceptual set, motion adaptation

Five different motion types were shown randomly interleaved. The target changed position with an SOA of 24, 71, 141, 282, or 565 ms. Four estimates of the PSE based on 18 trials were collected in a single session (360 trials). Each observer took part in two sessions in which either the line or the disk probes were used. The order of sessions with line and disk probes was balanced across observers. Thus, a total of eight estimates of the PSE were available for each motion type and observer. The trajectory length was either fixed at 4° or varied randomly

Table 2
Mean forward displacement in Experiments 1–3 expressed as the angle between the true and the judged final position in degrees of rotation

SOA (ms)	Experiment 1a–c (N = 24,12,12)	Experiment 1d (N = 22)	Experiment 2a (N = 19)	Experiment 2b (N = 14)	Experiment 3 (N = 14)
24/27	−0.54 (b)	−2.19†	4.74**	5.20**	1.54
71/80	–	−0.67	7.28**		3.61*
141/160	–	1.49	8.50**		4.90**
282/320	–	1.70	10.78**		6.01**
565/640	5.57** (a) 3.14* (c)	2.21†	11.73**	8.06**	6.35**
Intercept	–	−6.65**	−2.15*	2.21	−3.42†
Coefficient	–	3.38**	5.23**	2.08*	3.64**

Positive and negative numbers indicate displacement in and opposite to the direction of motion. The stimulus onset asynchrony (SOA) between successive target positions was varied. The SOAs varied slightly between experiments (see text). The log-transformed SOA was regressed on angular displacement for each observer. Mean intercepts and coefficients (between subjects) are reported.
Each mean was compared to zero by *t*-test. *T*-values with probabilities lower than $p < 0.10$, $p < 0.05$, and $p < 0.01$ are indicated by the symbols †, *, and **, respectively. Otherwise, the mean is not significantly different from zero ($p > 0.10$).

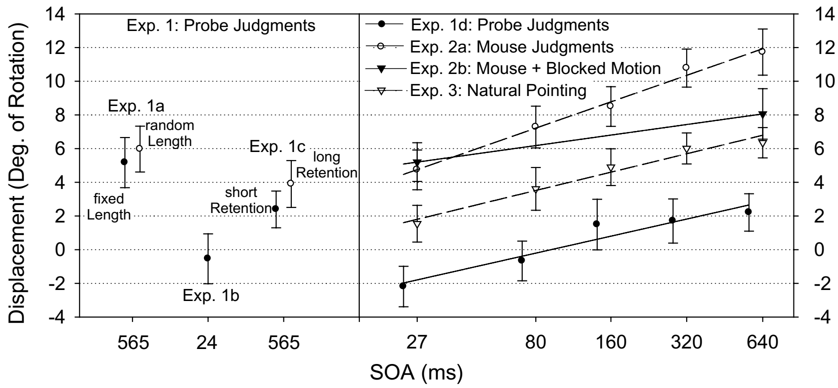

Fig. 3. Mean displacement in degrees of rotation in Experiments 1–3 as a function of stimulus onset asynchrony (SOA). Displacement was defined as the angle between the true and the judged final position. On a circle with a radius of 3° of visual angle, 10 degrees of rotation correspond to about 30 arcmin. Positive and negative numbers indicate displacement in and opposite to the direction of motion. In Experiment 1, only probe judgments were used. In Experiment 2, observers judged the final target position by adjusting a mouse cursor. In Experiment 3, they pointed to positions on a touch screen with their index finger. In Experiment 1a, the length of the trajectory was either fixed or varied randomly. In Experiment 1c, the retention interval was either 282 or 565 ms. In Experiment 2b, mouse judgments were used, but the motion type was blocked. The lines in the right graph are the regression lines of log-transformed SOA on forward displacement. The coefficients and intercepts are shown in Table 2.

between 2°, 4°, and 6°. Ten observers were presented with a fixed trajectory length, and twelve observers with a random trajectory length.

A mixed-factors ANOVA (variability of trajectory length × probe stimulus × SOA) did not reveal any effects of trajectory length (fixed or random) and probe stimulus (line or disk). However, there was a pronounced effect of motion type, $F(4,80) = 13.75$, $MSE = 110.4$, $p < 0.0001$, indicating that forward displacement increased with SOA. To determine the slope of the function, regressions of the log-transformed SOAs on forward displacement were run (see Table 2).

2.6. Discussion

The results are discussed with respect to the questions formulated in the introduction.

(1) *Effects of motion type*: Experiment 1a and b replicated the pattern of results observed in previous studies. Whereas reliable FD was observed with implied motion, no FD was observed with smooth motion. Experiment 1d demonstrates that the transition function between smooth and implied motion is continuous. That is, FD increased linearly with log-transformed SOA. Somewhat surprisingly, the weakest motion signals produce the strongest FD: With SOAs beyond the range of partial and apparent motion, FD was largest. This result rules out a simple hypothesis stating that FD is a dichotomous phenomenon: Based on the findings of Experiment 1a and b, one could argue that FD occurs whenever there is discontinuous motion (SOAs >30 ms) and disappears whenever motion appears smooth and continuous. The continuous increase of FD with SOA argues against such a hypothesis.

(2) *Motion adaptation*. There was no effect of probe stimulus. Although residual motion signals between target and probe were stronger with the disk-probe, no difference between disk- and line-probes emerged. This result provides first evidence against an explanation of forward displacement in terms of motion adaptation (Bertamini, 2002). In the following experiments, this preliminary result is further tested by using motor judgments that do not involve a probe stimulus at all.

(3) *Perceptual set*. The variability of the trajectory length had no effect on forward displacement arguing against a strong role of perceptual set. Similarly, FD was significant although direction of rotation and starting position were random. Previous research using a more complex stimulus found no FD under these conditions (Kerzel, 2002b). It may be that expectations about stimulus motion in a given trial are more important with complex motion types. That is, observers may have been unable to track target motion when a complex stimulus was shown and no information was available about where the stimulus appeared and moved to. With a simpler stimulus, less information about its motion may be necessary for successful tracking. This argument is consistent with the idea that the visual system creates an internal model of stimulus motion in some circumstances (Erlhagen, 2003) and that creation of this model failed with complex, incoherent motion. Nonetheless, there is some evidence for effects of perceptual set: Whereas there was highly significant FD with implied motion when only a single motion type was presented (Experiment 1a), FD with implied motion did not reach statistical significance when different motion types were randomly interleaved (Experiment 1d). Note that the latter result cannot be due to a lack of statistical power because the number of subjects was almost doubled in Experiment 1d ($N = 12$ vs. 22) and the number of repetitions collected per condition and subject was the same. Similarly, when the retention interval was chan-

ged—which also reduces observers' ability to predict the stimulus on a given trial—FD was also somewhat reduced. Thus, it appears that changing the nature of the display (SOA or retention interval) reduces FD. In contrast, knowledge about the motion trajectory does not affect FD.

3. Experiment 2a–b: Motor judgments (mouse)

In the present experiment, the response mode was changed from probe judgments to mouse pointing. In contrast to (symbolic, binary) probe judgments, mouse pointing involves goal-directed motor movements in space. Although the relation between hand/arm and cursor movements is rather artificial and arbitrary, it is nonetheless highly practiced for most people in an academic context. Therefore, it may be that pointing movements to the final target position involve processes that differ from those involved in probe judgments. Further, motor judgments do not require a probe stimulus such that an account of FD in terms of motion adaptation may be tested.

One problem for the comparison of probe and motor judgments is the retention interval. With probe judgments, the retention interval is well defined by the time interval between target offset and probe onset. With motor judgments, the situation is less clear. One possibility would be to define the retention interval as the time between target offset and the time when the movement reaches its goal. However, it is implausible that this is the most relevant time interval because the preparation (programming) of the goal-directed movement takes place well before the end state is reached. Thus, it is not clear what the retention interval is with motor judgments. However, this problem is somewhat alleviated because Experiment 1c showed that there was no time course of FD displacement with probe judgments. That is, after a retention interval of 250 ms, the remembered final position did not change significantly with further increases of retention interval (see also Finke & Freyd, 1985; Halpern & Kelly, 1993; Kerzel, 2002b).

3.1. General methods

3.1.1. Participants

Students at the Justus-Liebig-University of Giessen were paid for their participation. Participants reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment.

3.1.2. Stimuli and apparatus

A different apparatus was used. The stimuli were presented on a 17″ (diagonal) display with resolution of 1152 (H) $\times$ 864 (V) pixels and a refresh rate of 75 Hz. One pixel measured 2.1 arcmin. Target and background luminance was 0.5 and 43.3 cd/m^2, respectively. The horizontal position of one eye was monitored with a head-mounted, video-based eye tracker (EyeLink II, SR-Research, Canada). Observers' head position was stabilized with a chin rest. The stimuli were the same as in Experiment 2 with the following exception. A slightly larger black disk with a diameter of 42 arcmin was used as target. The target moved on a circular orbit with a radius of 3° at a slightly lower velocity of 3.1°/s. Because of the lower refresh rate of the monitor, the SOAs between successive stimulus presentations differed by a factor of 85 Hz/75 Hz = 1.13. The resulting SOAs were 27, 80, 160, 320, and 640 ms, such that the target position was changed at a frequency of 37.55, 12.5, 6.25, 3.13, and 1.56 Hz.

3.1.3. Procedure

Observers sat about 45 cm in front of the computer screen. Eye fixation was monitored and had to be maintained within 1° of the central fixation mark. Trials with fixation errors were not repeated. A white, cross-hair mouse cursor (23 $\times$ 23 arcmin) appeared 280 ms after target offset on the central fixation mark. Observers were asked to move the cursor to the final position of the moving target and to confirm their judgment by pressing a mouse button.

3.1.4. Results

The angle between the true and the judged onset position was calculated and is shown in Table 2 and Fig. 3. *T*-tests and regressions are shown in Table 2. Response latencies in Experiments 2–3 are shown in Table 3. Response latencies were defined as the time between onset of the mouse cursor and mouse click to confirm the judgment. Note that the mouse appeared 280 ms after target offset.

3.2. Experiment 2a: Motion type, perceptual set

The five different motion types were shown randomly interleaved. Starting position and direction of rotation were random. Observer worked through two blocks of 120 trials each for 48 repetitions per motion type. For ten observers, the trajectory length was fixed at 4°, and for nine observers, it varied randomly between 2°, 4°, and 6°.

With fixed trajectory length, 5.5% of the trials were excluded due to eye movements or blinks, and 7.8% with random trajectory length. A mixed-factors ANOVA (variability of trajectory length $\times$ SOA) showed that forward displacement increased with SOA, $F(4,68) = 52.84$, $MSE = 2.80$, $p < 0.0001$. Another two-way ANOVA (trajectory length $\times$ SOA) on the data from the variable trajectory condition showed that the length of

Table 3
Median response latencies in Experiments 2 and 3 (in ms)

SOA (ms)	Experiment 2a (mouse pointing)	Experiment 2b (mouse + blocked SOA)	Experiment 3 (real pointing)
27	1087 ± 88	995 ± 84	1133 ± 60
80	1128 ± 94	–	1162 ± 58
160	1146 ± 91	–	1206 ± 55
320	1262 ± 95	–	1319 ± 52
640	1336 ± 95	1050 ± 80	1463 ± 49

Median latencies were averaged across subjects. Mean and standard error of the mean (between-subjects) are given in the format (M ± SE). Latencies indicate the time between onset of the imperative signal and position judgment (mouse click or contact with the touch monitor). In Experiment 2, the imperative signal was the appearance of the mouse cursor (280 ms after target offset), in Experiment 3, it was the offset of the target stimulus.

the trajectory (2°, 4°, or 6°) did not affect forward displacement and did not interact with motion type.

Median latencies were computed for each participant and condition. A mixed-factors ANOVA (variability of trajectory length × SOA) showed that latencies decreased with SOA, $F(4,68) = 39.20$, $MSE = 5194.52$, $p < 0.0001$. No other effect was significant.

3.3. Experiment 2b: Motion type, perceptual set

Presentation of motion type was blocked. In one block, successive target positions were separated by an SOA of 27 ms. In the other block, the temporal separation was 640 ms. The order of blocks was balanced across observers and each block consisted of 80 trials. Motion direction and starting position were random, and trajectory length was fixed.

Due to fixation errors, 5.7% of the trials were excluded. Regressions of SOA on forward displacement were run for each observer. The resulting coefficients and intercepts defined a line between two data points (see Table 2). The mean coefficient was significantly different from zero ($M = 2.08$), $t(13) = 2.23$, $p < 0.05$, which is statistically the same as a significant difference of the condition means. Regression coefficients and intercepts of Experiment 2a and b were compared by t-test. The coefficients were significantly smaller with blocked than with randomly changing SOA, $t(18.1) = 3.59$, $p < 0.005$. Conversely, the intercepts were larger with blocked than with randomly changing SOA presentation ($M = 2.21$ vs. -2.74), $t(31) = -2.27$, $p < 0.05$.

Median latencies were 1091 and 1030 ms with SOAs of 27 and 640 ms, respectively. The difference was not significant.

3.4. Discussion

There were three main results.

(1) *Motion type/adaptation.* The increase of FD with increasing SOA was replicated. Because the experimental procedure excluded implied motion between target and probe stimulus, an explanation of the effect in terms of motion adaptation is unlikely.

(2) *Response mode.* FD was larger with mouse pointing responses than with probe judgments. Clearly, FD was significantly different from zero with all motion types. In particular, FD was significant with the smallest SOAs that gave an impression of smooth motion. In contrast, Experiment 1b as well as previous research (Baldo et al., 2002; Eagleman & Sejnowski, 2000; Kerzel, 2000; Whitney & Cavanagh, 2002; Whitney et al., 2000) demonstrated that FD was not significantly different from zero with smooth motion when probe judgments were used. The comparison between probe and motor judgments is complicated by numerous differences such as differences in retention interval, differences in the number of alternatives, etc. Nonetheless, the results suggest that motor processes use the motion signal in a different fashion. It may be that the motor system anticipates future target positions in order to overcome delays in transmission. This arguments reverses Nijhawan's (1994) original idea that the visual system extrapolates the position of moving objects in order to compensate for neural delays that would interfere with goal directed movements (i.e., catching): Not the visual system, but the motor system extrapolates the position of moving objects.

(3) *Response latencies.* Response times increased with SOA when the SOAs were randomly interleaved. With blocked presentation of SOAs, the response times were not different. Again, this effect brings up the issue of retention intervals. One may argue that the increase of FD with SOA was due to the increase in retention interval (i.e., response times) with SOA. However, this is unlikely as a similar increase of FD with SOA was found when retention intervals were fixed by using probe judgments (Experiment 1d). Nonetheless, the increase in response times may hint at the processes underlying FD. If observers imagined the next step in the sequence of position changes, this would take more time when the temporal separation of successive target positions is long. Therefore, response times would increase with SOA. An interpretation along these lines will be presented in Section 5.

4. Experiment 3: Motor judgments (natural pointing)

Experiment 3 was designed as a control for possible artifacts that arise from using the mouse as a pointing device. As laid out in Experiment 2, mouse pointing is a rather artificial movement such that it is unclear whether the results obtained with mouse pointing would generalize to more natural pointing movements. One crucial difference between mouse and natural pointing movements may be the relative weight of egocentric and allocentric position codes. Whereas mouse pointing involves moving a mouse cursor on the screen, that is, in an allocentric reference frame, natural pointing movements have to be coded with respect to the observer (i.e., in an egocentric reference frame).

4.1. Methods

4.1.1. Participants

Fourteen students participated.

4.1.2. Stimuli and apparatus

Stimuli and apparatus were the same as in Experiment 3 with the following exception. A 17″ (diagonal) touch screen was used that recorded contact with the screen at the pixel resolution of the monitor (i.e, 1152 H $\times$ 864 V). Target and background luminance was 1 cd/m^2 and 48.5 cd/m^2, respectively.

4.1.3. Procedure

Observers sat about 50 cm in front of the computer screen. Head movements were not constrained. Observers' task was to release a home key after target offset and to touch the final position of the target on the screen. If the home key was released earlier than 100 ms after target offset, the trial was discarded. Similarly, trials in which fixation was not maintained were excluded from the analysis.

4.1.4. Results

Data treatment was as in Experiment 2 and 5.0% of the trials were excluded due to fixation errors and anticipations. Means and regressions are reported in Fig. 3 and Table 2, respectively. A one-way ANOVA revealed that forward displacement increased with SOA, $F(4, 52) = 14.34$, $MSE = 3.72$, $p < 0.0001$. Forward displacement with mouse pointing (cf. Experiment 2a) and natural pointing movements were compared in a mixed-factors ANOVA (pointing response $\times$ SOA). Forward displacement was larger with mouse pointing responses, $F(1, 31) = 6.71$, $MSE = 102.23$, $p < 0.05$, and increased with SOA, $F(4, 124) = 59.32$, $MSE = 3.29$, $p < 0.0001$.

A further comparison of Experiments 2a and 3 showed that the regression coefficients were larger with mouse pointing than with real pointing movements ($M = 5.23$ vs. 3.64), $t(31) = 2.21$, $p < 0.05$, but the intercepts did not differ.

Latencies were defined as the time interval between target offset and contact with the screen. A one-way ANOVA showed that median latencies increased with SOA, $F(4, 52) = 81.66$, $MSE = 3152.89$, $p < 0.0001$.

4.2. Discussion

Overall, the results obtained in Experiment 2 were replicated. The size of FD and the increase of FD with SOA were somewhat reduced. However, FD was still larger compared to probe judgments (cf. Experiment 1d). Thus, there is no fundamental difference between pointing by moving a mouse cursor and natural pointing movements.

5. General discussion

The goals of the present study were threefold: First, the study looked at some methodological issues in the investigation of visual short-term memory. Previous studies did not control for effects of motion adaptation and perceptual set. It was argued that motion adaptation may explain FD (Bertamini, 2002) because a sequence of apparent motion elevates thresholds for the detection of motion in the same direction. If observers evaluated motion signals between the final target position and the probe position, presentation of implied motion would lead to more errors for probes presented in the direction of motion. However, varying the degree of implied motion between target and probe by using different probe stimuli (Experiment 1), and eliminating implied motion with motor judgments (Experiments 2 and 3) did not affect forward displacement. Therefore, an account of FD in terms of motion adaptation may be rejected.

Further, the variability of the trajectory length was manipulated to investigate effects of perceptual set, but this manipulation did not affect localization judgments in any of the experiments. However, some unexpected effects of experimental design were confirmed (see also Kerzel, 2002b): When implied motion was shown in isolation, robust FD was observed. When implied motion was randomly interleaved with other motion types, FD did not reach statistical significance even though statistical power was increased (Experiment 1a vs. 1d). Also, effects of motion type were reduced when a block design was used (Experiment 2a vs. 2b). Thus, the context of stimuli affected localization. Theses effects remain largely unexplained. In particular, it is unclear how "perceptual set" changes localization judgments. It may be that expectancy about which stimulus will appear in a given trial influences the criterion used to judge the final position. Alternatively, it may be that expectancy contributes to the processes producing the forward shift (i.e., extrapolation). Maybe it is easier to track the target motion with predictable and simple motion stimuli. The general pattern of results—larger FD with predictable motion—is somewhat contrary to effects of expectations on the flash-lag effect. For instance, it was found that the flash-lag effect is reduced when observers can anticipate the flash (Brenner & Smeets, 2000). Thus, the processes underlying the flash-lag illusion and FD in visual short-term memory may be different.

5.1. Effects of motion type

The second goal of the study was to investigate effects of motion type on FD. Taken together, previous studies suggested that FD occurs with implied stimulus motion but not with smooth motion. This suggestion was confirmed (Experiment 1a–b). Additionally, the current study manipulated the motion type by changing the SOA between successive target positions. Implied motion is characterized by large SOAs on the order of 500 ms, whereas smooth motion is characterized by SOAs smaller than 30 ms. The main result was that there is an increasing function relating SOA and FD. This result is unexpected for most models of position perception. Some recent models have suggested that the perceived position of a moving object is the result of integrating object positions over a relatively long temporal interval (Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 2000). Similarly, dynamic field theories of position perception would predict larger errors if the spatio-temporal contiguity between stimuli was increased (e.g., Erlhagen & Jancke, submitted for publication; Jancke et al., 1999). Because target positions were presented for half the SOA in the present experiments, the presentation time of single positions increased with SOA. Therefore, any errors due to temporal integration should be smaller for long SOAs. However, the opposite was the case: Localization of stimuli that were presented at the same position for 282/320 ms was less accurate than localization of stimuli presented for only 24/27 ms.

May be the most obvious interpretation for the effect of SOA is a variant of the mental extrapolation hypothesis: Observers (involuntarily) extrapolate the next position of the stimulus sequence after target offset and this overtracking of target positions leads to the error. Consistent with this assumption, response times in Experiments 2 and 3 increased with SOA as if observers imagined the next target step before responding. For long SOAs, the next step in the sequence is larger than for small SOAs (i.e., 2° with an SOA of 565 ms, 1° with an SOA of 282 ms, etc.). After extrapolating to the next step in the sequence, one may assume that observers compensate for this overshoot. That is, observers know that they have been asked to judge the final target position and not the next logical step in the sequence. The crucial assumption is that observers only compensate for part of the extrapolated distance such that judgments are biased toward the extrapolated position. Because the extrapolated distance increased with SOA, an increase of FD with SOA would result. As shown in Fig. 3, the relation between SOA and forward displacement is not linear. Therefore, the error is not a constant fraction of the step size. Rather, the increase of forward displacement with SOA decelerates. This is not surprising as one may assume that there are multiple mechanisms contributing to the localization of object position: First, a trace of the stimulus in visual short-term memory that is largely independent of the spatio-temporal context may be retrieved. Generally, localization of stimuli presented in isolation is highly accurate (e.g., Hansen, 1979; Hansen & Skavenski, 1985). Second, contextual cues may be used to localize an object. In the present case, observers may have localized the stimulus relative to the next (extrapolated) target position. However, errors induced by relative localization have an upper limit imposed by the accuracy of absolute localization. Therefore, the increase of FD with SOA tapers off.

In sum, one plausible explanation of effects of SOA on FD is that observers involuntarily extrapolate the next target position and do not fully compensate for this kind of "overtracking". This idea is consistent with the distinction between long-range and short-range motion (Braddick, 1980). Implied and smooth motion may be considered as variants of short- and long-range motion. Short-range (smooth) motion is likely to activate motion detectors that operate at a relatively low-level of motion detection (but see Cavanagh & Mather, 1989). In contrast, long-range (implied) motion has been associated with a more interpretative, cognitive mechanism that might identify forms (Zhuo et al., 2003) and then track their positions over time (Bex & Baker, 1999). The present data suggest that observers may not be able to stop tracking the target immediately, but go beyond the final target position. Conversely, if observers are unable to track target motion (i.e., to build and internal model of target motion) because it is highly unpredictable and complex, no overtracking and no FD occurs (Kerzel, 2002b).

Two findings support this idea. First, Finke and Shyi (1988) showed that observers are well able to extrapolate the next step in a sequence of complex long-range motion stimuli. Judgments showed a slight, but non-significant backward shift of the extrapolated target position, but were well-correlated with the true next target position. Second, a recent study measured the deployment of attention after implied motion (Kerzel, 2003a) and showed that attention moved beyond the final target position after target offset. In addition, FD was eliminated when attention was diverted from the final target position by presenting a distractor in the periphery. Thus, it may be that observers' attention follows the target and extrapolation is accomplished by moving attention to the next logical target position after target offset.

In contrast to previous theories of "representational momentum", the present account of FD provides a clear definition of what is meant by "mental extrapolation": Mental extrapolation refers to the anticipation of the next logical step in a sequence of position changes. In some of the previous studies, FD was attributed to internalized physical principles (overview in Hubbard, 1995b). It was assumed that there was a higher-order isomorphism between regularities in the physical world and the structure of mental representations. For instance, mental representations of dynamic events were considered to possess "representational" momentum, similar to the physical momentum of moving objects. Therefore, memory of the final position of a moving target would be biased forward because the representation itself would need some time to come to a halt. It is unclear how the notion of dynamic mental representations (see also Freyd, 1987) would account for effects of motion type (i.e., SOA). Given that the velocity of all motion types was the same, the inherent momentum of their representations would be the same.

The present data also challenge a strong version of the perceptual extrapolation hypothesis (Nijhawan, 1994). If the position of moving objects was extrapolated at a low level of processing, it would be difficult to explain why FD was absent with smooth motion. The target should have been *seen* at a position ahead of the true final position. Previous studies have shown that the absence of FD with smooth motion is stable across a large range of target velocities (e.g., Baldo et al., 2002; Eagleman & Sejnowski, 2000; Kerzel, 2000; Whitney et al., 2000). Therefore, a weaker version of the perceptual extrapolation hypothesis may state that extrapolation is not a universal phenomenon, but may occur in conditions that favor high-level motion processing. A similar conclusion was reached by Fu, Shen and Dan (Fu, Shen, & Dan, 2001). They found that blurred targets were perceived beyond the final target position. This was also true for target motion defined by contours (i.e., second-order motion). These targets are invisible to low-level motion detectors in V1 because features, not luminance differences are displaced. This suggests that high-level motion processing, presumably in V5, may account for perceptual extrapolation of the final position of blurred or contour targets.

Given these various effects of motion type on object localization, a possible direction for future research would be to determine differences in the localization of simple objects (i.e., the translation or rotation of a disk) and complex biological objects (e.g., point light walkers). Some recent work suggests that FD does obtain with smoothly animated natural scenes (Thornton & Hayes, in press) and observers are more sensitive to the next position of an animated sequence than to a previous one (Verfaillie & Daems, 2002).

5.2. *Effects of response mode*

Finally, the present experiments show that there is a difference between probe and motor judgments. Generally, FD was larger with motor responses than with probe judgments: In Experiment 2a and b, FD was significantly different from zero with all motion types, including smooth motion (SOA = 27 ms), whereas no FD was observed with smooth motion when probe judgments were used. In some respect, this finding contradicts the view that pointing movements have access to more veridical spatial information than probe judgments (Bridgeman, Lewis, Heit, & Nagle, 1979; Bridgeman, Peery, & Anand, 1997; but see Smeets & Brenner, 1995). In fact, pointing movements were shown to be less accurate than probe judgments in some conditions. However, the present results support the notion of distinct processes or representations serving motor actions and cognitive judgments (Goodale & Milner, 1992). It may be that the motor system anticipates future positions to a larger degree than the visual system. This argument would reverse the functional role assigned to extrapolation in previous studies (Freyd & Johnson, 1987; Nijhawan, 1994): The original argument was that the visual system extrapolates to provide goal-directed movements with an up-to-date representation of object position. In contrast, the present results suggest that extrapolation occurs in the motor system and to a lesser degree in the visual system. Thus, motor extrapolation may overcome processing delays inherent in the visual system.

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